

VEGETATION DYNAMICS, FIRE, AND THE PHYSICAL ENVIRONMENT IN COASTAL CENTRAL CALIFORNIA¹

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Abstract. Current concepts of vegetation dynamics include that of the shifting landscape mosaic, but evidence for shifting mosaics in disturbed and undisturbed systems is primarily based on negative spatial relationships among adults and recruits, and not on measurements of actual shifts over time. We used aerial photographs to measure transition rates as evidence for mosaic shifts among grassland, coastal sage scrub, chaparral, and oak woodland communities in central coastal California between 1947 and 1989. In unburned plots without livestock, transition from grassland to coastal sage scrub was 0.69% per year, coastal sage scrub to oak woodland was 0.30% per year, and oak woodland to grassland was 0.08% per year. These transition rates, considered together, indicate that vegetation patterns may be dynamic on landscapes dominated by these communities. In burned plots without livestock, and in unburned plots where livestock were not excluded, transition rates were lower, except for the conversion of oak woodland to grassland. In burned plots, a high rate of transition of coastal sage scrub to grassland was measured. Markov chain models predicted much less directional change in community proportions in either grazed or burned conditions than in ungrazed, unburned conditions. Some transition rates varied with substrate and topographical position, indicating that fire, grazing, and the physical environment interacted to determine direction and rate of vegetation change. Variation in transition on different substrates suggests that only portions of the vegetation of these landscapes may be dynamic, with some patches in certain combinations of environment and disturbance that change rapidly, and other patches that remain static as edaphic or topographic climax communities.

Key words: *coastal California plant communities; facilitation; fire; geographic information systems; grazing; landscape ecology; Markov models; shifting landscape mosaics; succession; vegetation dynamics.*

INTRODUCTION

Cyclical replacement of species in undisturbed plant communities was first proposed by Aubrevillé (1938), who observed that tree recruits in the pristine forests of western Africa seldom occurred under conspecifics. Such negative associations between adults and recruits have been reported as indirect evidence of cyclical succession in other undisturbed ecosystems including heathlands and beechwoods of Britain (Watt 1947), the Chihuahuan Desert (Yeaton 1978), the Mojave Desert (McAuliffe 1988), forests in eastern North America (Forcier 1975, Woods and Whittaker 1981), and forests in western and central Europe (Remmert 1991). Shifting mosaic and mosaic-cycle concepts of ecosystems were modelled by Clark (1991a, b) and reviewed by Remmert (1991). Although some direct evidence exists for large-scale landscape dynamics (e.g., Hall et al. 1991), the mosaic-cycle hypothesis in undisturbed ecosystems is based primarily on indirect evidence, predominantly the spatial relationships be-

tween adults and recruits. Also, most evidence for cyclical dynamics exists at the scale of individual adult trees, and there is little quantitative evidence for large-scale dynamic shifts among communities across landscapes in the absence of disturbance.

Coastal landscapes of central California are dominated by patchy mosaics of grassland, oak woodland, coastal sage scrub, and chaparral (Wells 1962, Griffin 1977, Heady 1977, Mooney 1977). Mosaics in some locations have been reported to correlate with geological substrate (Cole 1980) and soil characteristics (Harrison et al. 1971). However, Wells (1962) and Callaway and Davis (1991) found each of these physiognomic types represented abundantly on most soil depths, slope aspects, and all geological substrates. Lack of correlation between vegetation types and physical environmental factors suggests that disturbance or biological factors may have significant effects on the patchy distribution of vegetation types in central California.

Fire may initiate dynamic change in mediterranean-climate vegetation, and dynamic processes may differ in variable physical environments, but vegetation patterns in these mosaics also appear to be affected by complex species interactions. Callaway and D'Antonio (1991) found that seedlings of *Quercus agrifolia*, the

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dominant tree of coastal woodlands in California, were spatially associated with shrub communities, and that survival of experimentally planted seedlings was improved by shrub cover. They suggested that a sequence of nurse plant facilitation and oak-shrub competition may affect patterns and boundaries of these communities. Chaparral species have been reported to out-compete coastal sage scrub species for light, and to replace them successional (McPherson and Muller 1967, Hanes 1971, Gray 1983). Coastal sage scrub and chaparral shrubs suppress grass species (Muller and del Moral 1966, Bartholomew 1970, Halligan 1976), and some of the same grass species suppress growth of oak seedlings (Gordon et al. 1989). These types of biological interactions, acting in concert with natural disturbance, and variation in topography and substrate may produce complex transitional changes among community mosaics in central California.

We used direct measurements of vegetation mosaics on aerial photographs to quantify dynamic change in vegetation patterns and the relative importance of fire, livestock grazing, topography, and substrate in grassland, coastal sage scrub, chaparral, and oak woodland in central coastal California. Patterns of mosaics were compared on aerial photographs taken in 1947 and 1989, and transition rates were compared on unburned and burned land without livestock, unburned land with livestock, and on different geological substrates, soils, and topography.

STUDY AREA

The study was conducted at Gaviota State Park (34°28' N, 120°20' W), a 1120-ha coastal reserve 48 km west of the city of Santa Barbara extending ≈ 6 km inland. The terrain of the park rises from sea level to a maximum of 377 m in elevation over a 2-km distance and then gradually descends throughout most of the park as a complex combination of elevations, slopes, and aspects for ≈ 4 km with a minimum elevation of 85 m. The northeast corner of the park reaches 1440 m in elevation. The climate at Gaviota is mediterranean, with cool, wet winters and hot, dry summers; however, the climate of the southern portion of the park is directly affected by ocean winds and fog. Cattle grazing was eliminated in 1967 when the portion of the park where this study was conducted was incorporated into the state park system.

The geology of Gaviota State Park is complex, with the uplifted formations of the Santa Ynez Mountains as the predominant features. Surface geology is a mosaic of sandstone, shale, siltstone, and depositional material of 10 different formations (Dibblee 1988). Soils are also complex, with 23 different series recognized within the park. Excluding coastal strand vegetation, which we did not study, plant associations at Gaviota State Park can be categorized into four general communities based on species composition and the phys-

ionomy of the dominant species. Oak woodland is dominated by *Quercus agrifolia*, with understory dominants including *Bromus diandrus* Roth., *Avena fatua* L., and *Toxicodendron diversiloba* T. & G. Grasslands are dominated by *A. fatua*, *B. diandrus*, and *Brassica nigra* (L.) Koch, but *Stipa pulchra* Hitchc. is common in several small patches. The most common species in the semi-deciduous coastal sage scrub are *Artemisia californica* Less., *Salvia leucophylla* Greene, and *Baccharis pilularis* DC, and the two dominant species in the evergreen chaparral are *Ceanothus megacarpus* Nutt. and *C. spinosus* Nutt.

METHODS

Current distributions and transition rates

Community types in Gaviota State Park were mapped by interpreting 1:6000 true color aerial photographs acquired in August 1989, and vegetation polygons were directly transferred to 1:6000 base maps with acetate overlays. These maps were then digitized and the Geographic Information System ARC-INFO (Environmental Systems Research Institute, Redlands, California, USA) was used to calculate the area occupied by each community type in 1989. Over 90% of the polygons were checked in the field. Although these four communities can be more finely subdivided by species associations, we chose not to do so because of the difficulty of accurately identifying species on aerial photographs. The four types we chose represent basic physiognomic and taxonomic groups and were easily identified on black and white and color photographs.

Because transitional changes often occurred at scales too small to map and compare accurately with GIS (see Bolstad [1992] for discussion of error associated with air photograph relief and distortion in GIS analyses), we measured transitions among community mosaics with plots that were located directly on black and white 1947 aerial photographs and relocated on true color 1989 aerial photographs. One hundred thirty-one plots were stratified within Gaviota State Park by community type, and were located randomly within individual patches on a grid overlay. Plots were 2.5×2.5 mm squares that had been etched into the surface of a glass reticle. Plots were viewed through a $6\times$ magnifying lens. Approximately 0.25 ha of ground surface was sampled with each plot. To improve the accuracy of cover estimation each plot was subdivided into $25 \times 0.5 \times 0.5$ mm cells also etched into the reticle (100 m² of ground surface). Cover of grassland, coastal sage scrub, chaparral, and oak woodland was estimated by 10% classes within each cell and summed for plot totals. After cover was estimated within a plot on the 1947 photograph, the plot was relocated on the 1989 photograph by triangulating to each corner of the plot from nearby landmarks. Ten plots were relocated three times each to estimate errors in placement. In each case, cover estimates varied by $<5\%$. Prior to mea-

surement, the distance between two landmarks near each prospective plot was measured on the 1947 and 1989 photographs to estimate differences in distortion. If the measurements between landmarks differed more than 5% between photographs, then plots were not used. Despite these precautions, overestimation of within-plot transition can be large due to small differences in plot location between sample dates. To reduce overestimation of within-plot transitions we recorded all transition rates within an individual plot as zero unless the *cumulative* transition between one vegetation type and another exceeded 10% of the original area in 1947. For example, if 10% of chaparral converted to oak woodland and 10% of oak woodland converted to chaparral, we recorded the transition as zero. If 20% of chaparral converted to oak woodland and 10% of oak woodland converted to chaparral, the transition was 10%.

Transition rates were calculated for plots that had not burned since 1929 or earlier ($n = 78$), and for plots that had been burned in 1944, 1955, or 1986 ($n = 53$). Burned plots were combined in order to achieve an adequate sample size. Fires were mapped using historical fire records obtained from the United States Forest Service. We also measured transitions in 89 other plots randomly located outside the borders of Gaviota State Park on unburned land and where livestock were not excluded. Areas of community types outside of the park were not measured. We report transitions as annual rates for each of the three disturbance regimes that were calculated by dividing the total rates by 42, the number of years elapsing between sample dates.

Transition rates were compared on variable topography, geological substrates, and soils. Topography was summarized for each plot by calculating an index of northness (N) as

$$N = \cos(\text{azimuth}) \times \sin(\text{slope}),$$

where azimuth is measured as degrees from north (Borchert et al. 1989). Thus steep north-facing slopes had high northness indices (>0.20) and steep south-facing slopes had low northness indices (<-0.20). West-facing, east-facing, or relatively level topography had intermediate northness indices. The relationship between northness and transition rates was evaluated by calculating Pearson's correlations for northness and each transition rate of 0.08% per year or higher. Geological formations were grouped into four major types: sandstone, depositional, shale, and siltstone as mapped by Dibblee (1988). Soils were grouped into four general classes based on texture and drainage characteristics as described and mapped by Shipman (1972, 1977). The soil classes used were rocky, excessively drained soil; sand to silty sand highly drained soil; loamy well-drained soil; and silty clay to clay moderately drained soil. Substrate and topography classes were determined

for each plot. All comparisons among transition rates were conducted by ANOVA or with Student's t test using transformed ($\log[x + 1]$) rates.

Markov chain models

Markov chain models have been used with transition rates such as we have measured to predict transitional rates of succession in eastern forests of North America (Horn 1975, Hall et al. 1991) and the Mojave Desert (McAuliffe 1988). Such models are useful for general predictions of changes taking place from one state to another, but they assume that measured transition rates approximate future transition rates (see Barbour et al. [1987] and McAuliffe [1988] for descriptions of technique). We used transition rates to predict the values of future states (cover of community types) by multiplying 42-yr transition rates (the time span of our sampling period) by each of the four current states (areas of space occupied by a community type, derived from the ARC-INFO map). Multiplication of each current state by transition rates for the current state to each other current state yielded the proportions of a new current state at time 2 (in this study, 42 yr). The state at time 2 was multiplied by transition rates to yield new proportions for the state at time 3 (84 yr) and so on. We used transition rates derived from plots outside the park with current areas of vegetation types inside of the park to estimate future states in the presence of livestock.

RESULTS

Current distributions and transition rates

The four community types were highly intermixed throughout Gaviota State Park. Based on the GIS vegetation map, plots provided a representative sample of upland vegetation in the park (Fig. 1). Mapped proportions of types were: grassland 21.5%, coastal sage scrub 26.4%, chaparral 28.0%, and oak woodland 24.1%. In comparison, plot composition in 1989 was: grassland 23.3%, coastal sage scrub 25.9%, chaparral 24.0%, and oak woodland 26.8%. Frequencies of plots (classified by their dominant community type) on different topography, geology, and soils for all 220 plots are presented in Fig. 2. Community types were relatively widespread across environmental variables with a few exceptions. Chaparral was common on sandstone, absent from depositional material, and was restricted to rocky and sandy soil. Grassland was more common on depositional material and less common on rocky soil than other communities. Chaparral was more common at both extremes of the northness index than at intermediate levels because of its association with steep slopes. Oak woodland was positively associated with northness, and grassland and coastal sage scrub were associated with more south-facing topography. Although these communities were partially as-

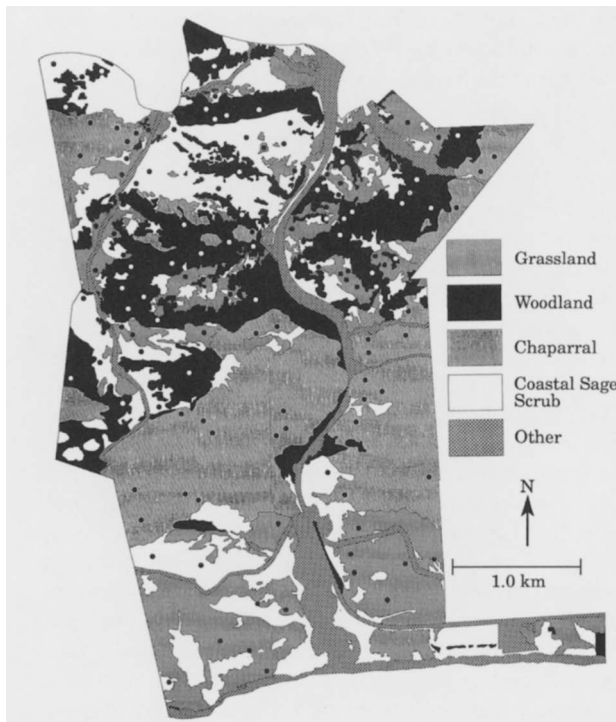


FIG. 1. Map of grassland, coastal sage scrub, chaparral, and oak woodland vegetation mosaics at Gaviota State Park (California). Plot locations are designated by black dots on light backgrounds and white dots on dark backgrounds.

sociated with environmental factors, in most cases they were widely distributed across a variable environment.

Transitional change occurred in 71 of the 220 plots. In unburned, ungrazed plots, high transition rates were recorded among several community types (Fig. 3). In unburned and ungrazed grassland, 23 of 43 plots underwent at least partial conversion to coastal sage scrub, yielding a transition rate of 0.69% per year. Coastal sage scrub, in unburned and ungrazed plots, was often replaced by oak woodland (0.30%/yr, 10 of 34 plots) and chaparral (0.11%/yr, 5 of 34 plots). Transition rates from chaparral to oak woodland were 0.12%/yr, and occurred in 4 of 14 plots. Oak woodland converted to grassland at 0.08%/yr. Other transition rates were very low. Based on transition rates measured over the 42-yr measurement period, area occupied by grassland declined by 27.4%, and coastal sage scrub, chaparral, and oak woodland increased by 27.1%, 5.4%, and 10.0%, respectively, in unburned and ungrazed plots.

For plots within the park that had burned in 1944, 1955, or 1986, transition rates (Fig. 4) were substantially different than for unburned plots. Transition rates from grassland to coastal sage scrub was 66% lower (t test with $\log(x + 1)$ -transformed rates, $n_{\text{burned}} = 23$, $n_{\text{unburned}} = 43$, $t = 2.22$, $df = 64$ for plots with grassland, $P = .03$), while coastal sage scrub transition to grassland increased from 0.04 to 0.31% per year (t test with $\log(x + 1)$ -transformed rates, $n_{\text{burned}} = 14$, $n_{\text{unburned}} = 34$, df

$= 46$ for plots with coastal sage scrub, $t = 2.41$, $P = .02$). Transitions of coastal sage scrub to chaparral and chaparral to oak woodland were not observed in burned plots. Transition from oak woodland to grassland was the only large transition rate that did not differ between burned and unburned plots.

Most of the transition rates in unburned plots outside of Gaviota State Park (Fig. 5), which were exposed to livestock grazing, were different than unburned plots within the park. Transition from grassland to coastal sage scrub outside of the park was 72% less than inside of the park in unburned plots (t test using $\log(x + 1)$ -transformed rates, $n_{\text{within park}} = 43$, $n_{\text{outside park}} = 34$, $t =$

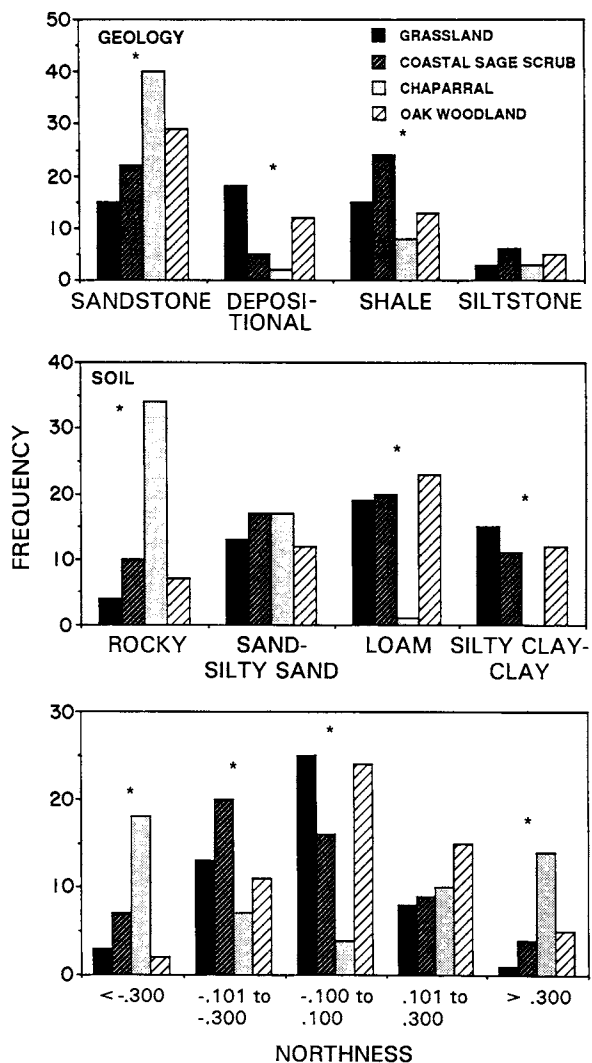


FIG. 2. Frequencies of plant community types in all plots combined ($n = 220$) sampled on aerial photographs of Gaviota State Park acquired in 1989. Observed distributions of samples on a substrate or topography class that differ significantly from expected distributions based on mapped areas, using a geographic information system (chi-square tests, $P < .05$. Tests were conducted separately for each class, and frequencies can be found in the figure).

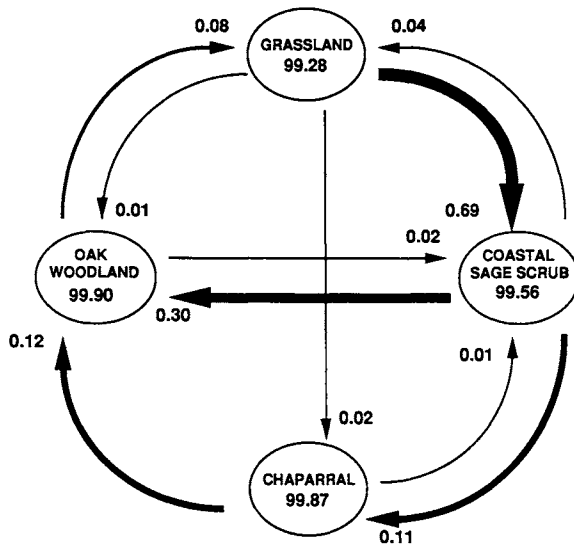


FIG. 3. Annual transition rates among plant communities in unburned plots ($n = 78$) with livestock excluded within Gaviota State Park, as determined from changes in vegetation between 1947 and 1989 shown on aerial photographs. The numbers in the ovals estimate the probability, as a percentage, that a given community will remain the same; the numbers on the arrows estimate the probability that a community will change in the indicated direction (thickness of lines is proportional to the probability of that change).

3.49, $df = 75$, $P < .0001$). Transition rates from coastal sage scrub to oak woodland and from chaparral to oak woodland were not significantly different than those inside the park in unburned plots. Transition from oak woodland to grassland was very similar to that in both burned and unburned plots in the park.

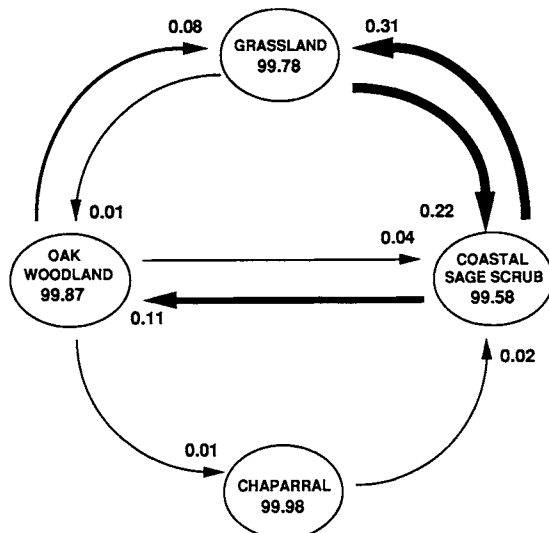


FIG. 4. Annual transition rates among plant communities in burned plots ($n = 53$) with livestock excluded within Gaviota State Park, as determined from changes in vegetation between 1947 and 1989 shown on aerial photographs. Numbers as explained in Fig. 3.

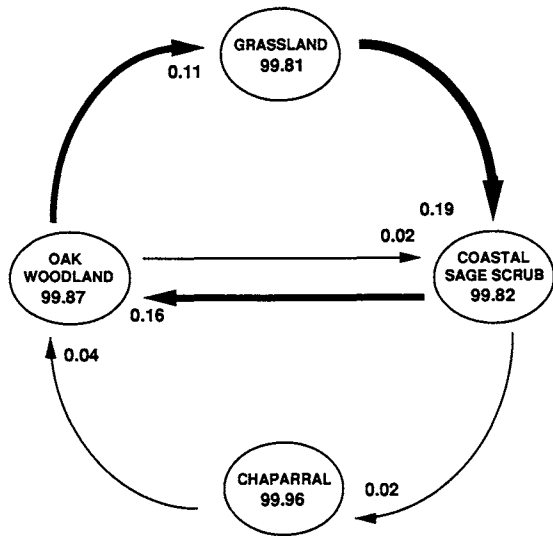


FIG. 5. Annual transition rates among plant communities in unburned plots ($n = 89$) outside of Gaviota State Park exposed to livestock grazing, as determined from changes in vegetation between 1947 and 1989 shown on aerial photographs. Numbers as explained in Fig. 3.

Physical environment and transition rates

In unburned plots within the park, transition from grassland to coastal sage scrub was similar on all geological types (Table 1). Transition rates of grassland to coastal sage scrub within the park were lower in burned plots than in unburned plots, but the effect of burning varied with geological substrate. On depositional and shale substrates the transition from grassland to coastal sage scrub was significantly lower in burned plots than in unburned plots. Significantly higher conversion of coastal sage scrub to oak woodland occurred on siltstone in comparison to sandstone and shale, and the transition from coastal sage scrub to grassland on burned plots proceeded more rapidly on depositional substrates than on other geological types.

Transition rates from grassland to coastal sage scrub were similar on all soil types in unburned and ungrazed plots (Table 2). In burned plots, however, transition rates on silty clay to clay soil were significantly lower than all soil types in unburned and ungrazed plots, which suggests that fire limited shrub invasion more effectively in combination with clay soils. The transition of chaparral to oak woodland occurred much more frequently on highly drained sandy soil than on excessively drained rocky soil. Although soil classes did not coincide completely with geological types, excessively drained rocky soils were usually associated with sandstone, and moderately drained silty clay to clay soils tended to be associated with depositional and siltstone geological formations.

Transition rates outside of the park were similar on most substrates (Tables 1 and 2), but several substrate-

TABLE 1. Annual transition rates between plant community types (in percentage per year) for major transitions on different geological substrates in burned and unburned plots in Gaviota State Park, and in unburned plots adjacent to Gaviota State Park, California. * n = sample size and the sum of the n 's may exceed total sample size (n = 220) because multiple transitions occurred within single plots.

Substrate type	Community type‡ transition							
	Grass → CSS		CSS → Chap		CSS → Oak		Chap → Oak	
	$\bar{X} \pm 1 \text{ SE}$	n	$\bar{X} \pm 1 \text{ SE}$	n	$\bar{X} \pm 1 \text{ SE}$	n	$\bar{X} \pm 1 \text{ SE}$	n
Unburned, in park								
Sandstone	0.54 ± 0.17^{ac}	15	0.12 ± 0.09^a	15	0.13 ± 0.11^{ab}	15	0.19 ± 0.11^a	10
Depositional	0.78 ± 0.27^a	4
Shale	0.80 ± 0.23^a	23	0.09 ± 0.09^a	15	0.08 ± 0.08^a	15	0.12 ± 0.11^a	4
Siltstone	1.13^\dagger	1	0	4	0.70 ± 0.21^b	4
Burned, in park								
Sandstone	0.47 ± 0.40^{ab}	8	0	6	0.28 ± 0.10^a	6	0	14
Depositional	0.25 ± 0.09^b	8	0	3	0	3	0	1
Shale	0	7	0	5	0	5	0	4
Siltstone	0	3
Unburned, adjacent to park								
Sandstone	0.12 ± 0.03^b	8	0.04 ± 0.04^a	14	0.21 ± 0.06^a	14	0.02 ± 0.02^a	19
Depositional	0.11 ± 0.05^b	13	0	5	0	5	0.46^\dagger	1
Shale	0.26 ± 0.11^{bc}	9	0	10	0.20 ± 0.11^a	10	0	1
Siltstone	0.20 ± 0.12^b	6	0	3	0	3

* Shared superscript letters within a transition class indicate no significant difference as determined by ANOVA and post-ANOVA Tukey HSD tests ($P < .05$); † indicates too few samples for statistical comparisons, and ... indicates that no samples occurred on the transition-substrate combination.

‡ Grass = grassland, CSS = coastal sage scrub, Chap = chaparral, Oak = oak woodland.

related differences were found. Conversion of coastal sage scrub to oak woodland and oak woodland to grassland was higher on loamy soils than on others, and conversion of oak woodland to grassland was highest on siltstone substrates. Conversion of grassland to coastal sage scrub was lower outside of the park than inside of the park on all substrates.

Most transition rates were not significantly correlated with northness (Table 3); however, coastal sage scrub

transition to chaparral was negatively correlated with northness, which suggests that chaparral shrubs invade coastal sage scrub more rapidly on exposed, south-facing slopes than on sheltered topography. Conversely, the transition of coastal sage scrub to oak woodland in unburned plots was correlated with northness. These correlations did not occur in burned plots, which suggests that fire may have eliminated any dynamic trends that were dependent on topography.

TABLE 2. Annual transition rates between plant community types (in percentage per year) for major transitions on different soil substrates in burned and unburned plots in Gaviota State Park, and unburned plots adjacent to Gaviota State Park, California. Data presentation as in Table 1.

Soil type	Community type transition							
	Grass → CSS		CSS → Chap		CSS → Oak		Chap → Oak	
	$\bar{X} \pm 1 \text{ SE}$	n	$\bar{X} \pm 1 \text{ SE}$	n	$\bar{X} \pm 1 \text{ SE}$	n	$\bar{X} \pm 1 \text{ SE}$	n
Unburned, in park								
Rocky	1.12 ± 0.45^a	6	0.36 ± 0.17	10	0.27 ± 0.11^{abc}	10	0.02 ± 0.02^a	10
Sand-silty sand	0.73 ± 0.26^a	8	0	8	0.28 ± 0.19^{abc}	8	0.40 ± 0.14^b	4
Loam	0.60 ± 0.20^a	19	0	11	0.47 ± 0.17^a	11
Silty clay-clay	0.71 ± 0.25^a	10	0	5	0	5
Burned, in park								
Rocky	0	1	0.49^\dagger	1	0	17
Sand-silty sand	0.31 ± 0.27^{ab}	12	0	8	0.12 ± 0.02^{bc}	8	0	5
Loam	0.46 ± 0.34^{ab}	3
Silty clay-clay	0.08 ± 0.07^b	8	0	5	0	5
Unburned, adjacent to park								
Rocky	0.37^*	2	0.13 ± 0.13^a	5	0.11 ± 0.06^{bc}	5	0	12
Sand-silty sand	0.19 ± 0.07^b	9	0	10	0	10	0.09 ± 0.05	9
Loam	0.16 ± 0.05^b	15	0	16	0.28 ± 0.06^{ab}	16
Silty clay-clay	0.16 ± 0.10^b	10	0	1	0	1

TABLE 1. Continued.

Community type‡ transition			
Oak → Grass		CSS → Grass	
$\bar{X} \pm 1 \text{ SE}$	<i>n</i>	$\bar{X} \pm 1 \text{ SE}$	<i>n</i>
Unburned, in park			
0.09 ± 0.01 ^{ab}	22	0	15
0	1
0.05 ± 0.05 ^a	9	0.06 ± 0.06 ^a	15
0	4	0	4
Burned, in park			
0.07 ± 0.05 ^{ab}	9	0.14 ± 0.06 ^a	6
0.37†	2	1.15 ± 0.20 ^b	3
0	3	0	5
...
Unburned, adjacent to park			
0.04 ± 0.03 ^a	13	0	14
0.13 ± 0.07 ^{ab}	7	0	5
0.11 ± 0.07 ^{ab}	5	0	10
0.28 ± 0.09 ^b	3	0	3

Markov chain models

Markov chain models based on measured transition rates predicted substantial differences in the changes in proportional cover of oak woodland and grassland in the absence of fire (Fig. 6). In unburned and ungrazed plots the initial area occupied by grassland was predicted to decrease rapidly as coastal sage scrub invaded grassland and in turn was replaced by woodland. When transition rates that were derived from burned plots were used in Markov chain models with the same current states (community areas), predicted changes were

TABLE 2. Continued.

Community type transition			
Oak → Grass		CSS → Grass	
$\bar{X} \pm 1 \text{ SE}$	<i>n</i>	$\bar{X} \pm 1 \text{ SE}$	<i>n</i>
Unburned, in park			
0	7	0	10
0.09 ± 0.06 ^a	10	0.15 ± 0.08 ^a	8
0.12 ± 0.08 ^a	14	0	11
0	5	0	5
Burned, in park			
0.04†	1
0.05 ± 0.05 ^a	9	0.07 ± 0.07 ^a	9
...
0.18 ± 0.18 ^a	4	0.76 ± 0.20 ^a	5
Unburned, adjacent to park			
0	4	0	4
0	9	0	10
0.22 ± 0.04 ^a	14	0	16
0	1	0	2

qualitatively and quantitatively different (Fig. 6). In these plots, grassland increased, coastal sage scrub decreased, and chaparral and oak woodland remained relatively stable. The general directions of changes that were predicted for unburned plots outside of the park were similar to those predicted for unburned within the park, but with much lower increases in oak woodland and decreases in grassland.

DISCUSSION

Over a 42-yr period, from 1947 to 1989, substantial conversion of grassland to coastal sage scrub, coastal sage scrub to chaparral and oak woodland, chaparral to oak woodland, and oak woodland to grassland was measured on aerial photographs of unburned vegetation. These transition rates indicate that vegetation patterns in the study area are dynamic, and that biotic interactions may determine a dynamic "shifting mosaic" landscape (e.g., Clark 1991a) even in the absence of large-scale disturbance. If these transition rates continue for a long period of time, and if each occurs in the same location over time, cyclical succession among these community types will occur (e.g., Watt 1947, Yeaton 1978, Bormann and Likens 1979, Remmert 1991). Cycles of interspecific patterns of replacement have been documented in forest and desert communities (Forcier 1975, Woods and Whittaker 1981, McAuliffe 1988), but these appear to result in sequential changes in the occupancy of a small area by individual plants (McAuliffe 1988) and not a shifting mosaic of communities. We only measured transitions between two points in time, and thus we could not directly observe multiple, cyclical shifts at a single location. However, grassland to coastal sage scrub to oak woodland to grassland transitions were all found on sandy and loamy soils, and on sandstone and shale geological types, suggesting that a cycle of these transitions is possible. Similarly, Wells (1962) found each of the four physiognomic types studied here represented abundantly on most soil depths, slope aspects, and all geological substrates elsewhere in California.

Similar vegetation dynamics have been reported elsewhere in mediterranean-climate vegetation. For example, grasslands in mediterranean ecosystems in California have been reported to convert to shrublands (McBride and Heady 1968, Biswell 1974, McBride 1974, Westman 1976, Scheidlinger and Zedler 1980, Johnson and Fitzhugh 1990). Mediterranean grasslands and oak savannas in the Sierra Norte of Spain are also rapidly converted to shrubland without fire, and have been reported to have decreased 34% between 1956 and 1977 in the region, while shrublands have increased 73% during the same time (Joffre et al. 1988). Oaks invade shrubland in other locations in California (McBride 1974, Scheidlinger and Zedler 1980, Short and Short 1987) at rates apparently affected by fire frequency (Wells 1962, Wilson and Vogl 1965, Vogl 1981). Coastal sage scrub species in other locations in

TABLE 3. Pearson's correlations between northness and transition rates between plant community types at Gaviota State Park, California, under three different conditions. ... indicates that no transition occurred under the specific fire or grazing regime.

	Community type† transition					
	Grass → CSS	CSS → Chap	CSS → Oak	Chap → Oak	Oak → Grass	CSS → Grass
Unburned, ungrazed						
Northness	-0.08	-0.41*	0.46*	0.23	-0.06	...
Burned, ungrazed						
Northness	-0.25	...	-0.07	...	-0.13	0.05
Unburned, grazed						
Northness	0.17	-0.25	0.54*	0.29	-0.23	...

* $P < .05$.

† Grass = grassland, CSS = coastal sage scrub, Chap = chaparral, Oak = oak woodland.

central California have been reported to be replaced by chaparral species (McPherson and Muller 1967, Gray 1983), and *Rhus integrifolia*, a large evergreen, sclerophyllous shrub, recruits into and may replace coastal chaparral dominated by other species (Lloret and Zedler 1991).

The patterns of vegetation dynamics we observed corroborate those reported by McBride (1974), who found that grassland in the Berkeley Hills of California had been replaced by *Baccharis pilularis*, a common

invasive shrub at our study site, which in turn was replaced by *Q. agrifolia*. He hypothesized that *Q. agrifolia* woodlands would eventually be replaced by *Umbellularia californica*, an event that was not documented at Gaviota State Park. Our results are also supported by Short and Short (1987), who used a time series of aerial photos to document conversion of *Q. agrifolia* woodland to grassland, and invasion of *Q. agrifolia* into contiguous chaparral communities. Scheidlinger and Zedler (1980) also documented relatively high transition rates for grassland conversion to shrubland, shrubland conversion to *Q. agrifolia* woodland, and *Q. agrifolia* woodland conversion to grassland in southern California.

Although Markov chain models predicted only moderate cumulative changes in proportions of coastal sage scrub at Gaviota State Park, this highly transitional community appeared to affect transitions between grassland and oak woodland. Chaparral and oak woodland rarely replaced grassland directly, but both rapidly replaced the coastal sage scrub that directly replaced grassland. Facilitation of *Quercus* species by shrubs in central California also has been reported elsewhere. Callaway and D'Antonio (1991) and Callaway (1992) found that *Q. agrifolia* and *Q. douglasii* seedlings were spatially associated with shrubs, and that survival of experimentally planted seedlings was enhanced by shrub canopies. Shrubs appeared to ameliorate climatic extremes and to protect oak seedlings from predators. Shrubs may also eliminate grasses (Muller and del Moral 1966, Bartholomew 1970, Halligan 1976), which can strongly suppress oak seedlings (Gordon et al. 1989, Danielson 1990), thus indirectly facilitating seedling survival. Oaks may replace shrubs by eventually overtopping and shading them (C. M. Callaway, *personal observation*), creating a subcanopy environment favorable for grass species, including *Bromus diandrus* (Parker and Muller 1982), which is also common in open grassland.

During the 42-yr sample period $\approx 4\%$ of oak woodland converted to grassland in both unburned and burned parts of the park. This transition occurred at

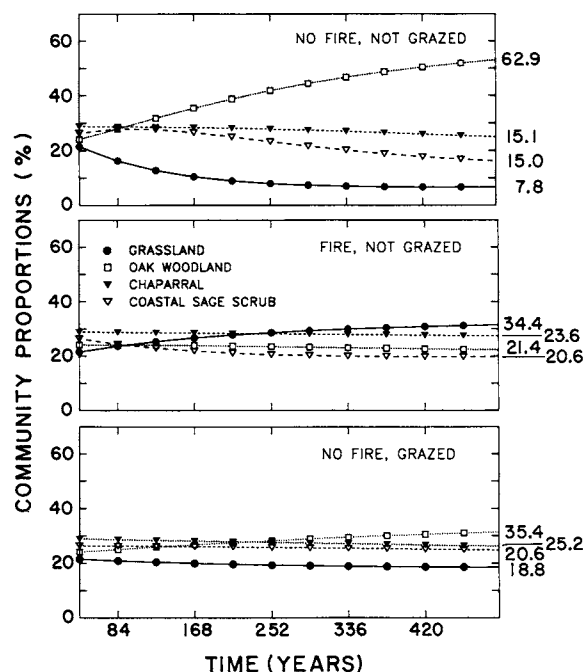


FIG. 6. Markov chain model predictions of future change in proportions of plant communities at Gaviota State Park, based on transition rates calculated between 1947 and 1989 and the areas of plant communities existing in 1989. Predictions for unburned, grazed conditions were based on transition rates measured in plots located outside, but adjacent to, Gaviota State Park and areas of communities within the park. Final community proportions at stability (defined as $<0.1\%$ change over 42 yr) are presented at the right, opposite each curve.

similar rates outside of the park, and has been documented by others in *Q. agrifolia* woodlands in other locations (Scheidlinger and Zedler 1980, Short and Short 1987). If transition of woodland to grassland occurs in the same locations as other transitions, it completes a cycle of succession from grassland to coastal sage scrub to oak woodland and back again to grassland. Without significant disturbance, the transition of oak woodland to grassland could not occur if oak seedlings regenerated adequately under conspecific adult oaks. Poor oak seedling regeneration is common in woodlands dominated by *Q. agrifolia* in central California (Muick and Bartolome 1987, Callaway and D'Antonio 1991). Regeneration of conspecific seedlings under adult oaks may be limited by natural predators (Griffin 1976, Borchert et al. 1989), livestock grazing (Borchert et al. 1989), or suppression by adult oaks (Runov and Egorova 1962), although no specific mechanism has been investigated in *Q. agrifolia* woodlands. In this study we considered all woodland dominated by *Q. agrifolia* to be a homogenous species association; however, R. M. Callaway and F. W. Davis (*unpublished data*) found that *Q. agrifolia* woodlands at Gaviota State Park consisted of two distinct groups based on species composition. Woodland with herbaceous understories and on gently sloping topography had very low seedling and sapling densities, and thus appeared likely to convert to grassland after the death of the adult oaks, whereas woodlands with shrub understories and on north-facing slopes had substantial densities of young oaks and may remain oak woodlands in the future.

Transition rates derived from burned plots indicated that fire strongly altered vegetation dynamics, primarily by reducing the invasion of grassland by coastal sage scrub and converting coastal sage scrub back to grassland. McBride and Heady (1968) reported that low fire frequency in grasslands in northern California resulted in an increase in *Baccharis pilularis* shrublands from 7% to 22% in 30 yr. In the absence of fire, Westman (1976) documented the replacement of undisturbed grassland by coastal sage scrub within 13 yr, a rate higher than we observed at Gaviota State Park. Transition rates of coastal sage scrub to oak woodland were lower in burned plots, and oak replacement of chaparral was eliminated in burned plots. Fire frequency is correlated with low proportions of *Q. agrifolia* in other California shrublands (Wells 1962, Griffin 1978, Davis et al. 1988). *Quercus agrifolia* resprouts vigorously after fires (Lathrop and Osborne 1991), and so establishment where fires are frequent is probably limited by the intolerance of acorns and seedlings to fire and by slow postburn dispersal of acorns. Zedler et al. (1983) found that frequent fire appeared to favor the expansion of coastal sage scrub into areas occupied by chaparral. We did not observe substantial conversion of chaparral to coastal sage scrub, but in burned areas the transition of coastal sage scrub to chaparral was eliminated.

Markov chain predictions suggest that fire stabilizes the relative areas occupied by grassland, coastal sage scrub, chaparral, and oak woodland at roughly equal proportions at Gaviota State Park, but Markov predictions derived from plots without fire or grazing suggested that oak woodland would dominate a much greater proportion of the landscape without disturbance (also see Wells 1962).

On landscapes subjected to grazing by livestock, dynamic change from grassland to coastal sage scrub to oak woodland was also evident, but it progressed at a lower rate, primarily due to low conversion rates of grassland to coastal sage scrub. However, directional changes that were predicted by the Markov chain model under unburned, grazed conditions were similar to those predicted under unburned, ungrazed conditions. Thus grazing appears to slow the rates at which community types may replace each other, but, unlike fire, does not alter the direction of succession. Considerable evidence indicates that grazing prevents grassland from converting to shrubland in California (McBride and Heady 1968, McBride 1974, Minnich 1981, Johnson and Fitzhugh 1990), and in mediterranean Europe (Joffre et al. 1988). Vogl (1976) and Axelrod (1978) proposed that coastal sage scrub is a community that is maintained by disturbance, and is dependent on anthropomorphic alteration of grassland. Our evidence suggests the contrary with regard to coastal sage scrub and grassland. We found that disturbance in grassland (either fire or grazing) limits invasion of coastal sage scrub species. With regard to coastal sage scrub and chaparral interactions, however, we found that disturbance may maintain coastal sage scrub distribution by preventing its invasion by chaparral species. This is consistent with the findings of Gray (1983) and McPherson and Muller (1967).

We found substantial cumulative transition rates across a wide variety of topographical, geological, and soil conditions, but we also found evidence for interaction among the physical environment, fire, and the biological interactions that affect vegetation dynamics on undisturbed landscapes (*sensu* Pickett et al. 1987, De Steven 1991). In the absence of fire, shrubs invaded grassland on moderately drained silty clay to clay soils at rates similar to those on other soil types. In burned plots, however, shrub invasion of grassland on silty clay to clay soils was significantly lower than on the other soil types, which suggests that soil characteristics and fire disturbance interactively affect transition rates. Similar interactions appeared to occur for grass to coastal sage scrub transitions, fire, and shale substrates. Wells (1962) also reported vegetation patterns in central California that appeared to be determined by interactions between disturbance and substrate. Soil and fire-related changes in vegetation have also been reported in the bluestem prairie of Kansas, where shrub invasion proceeds much more rapidly on clay loam soils than coarser textured soils when fires are infre-

quent (Bragg and Hurlbert 1976). High correlations between northness and transition rates from coastal sage scrub to chaparral and oak woodland occurred only in unburned plots, which indicates that topography may also interact with fire to affect vegetation dynamics.

Interactions among biology, disturbance, and the physical environment suggest that some patches in the vegetation mosaic change rapidly, while other patches, which appear identical in species composition, may remain in place for long periods of time (see Biswell 1974, Bradbury 1974, Cole 1980, Zedler et al. 1983, Davis and Mooney 1985). For example, the overall transition rate of chaparral to oak woodland in plots without fire was 0.12%/yr. On excessively drained rocky soils, however, where over 75% of chaparral was found, the rate was negligible. Thus chaparral on rocky soils may remain chaparral indefinitely as an edaphic climax community, while patches of chaparral on less rocky soil may be transitional in the absence of fire. Similarly, coastal sage scrub that occurs on moderately drained silty clay to clay soil (about 30% of coastal sage scrub sampled) was not replaced by oaks or chaparral as were large percentages of coastal sage scrub on other soil types, and as such may also constitute an edaphic climax community. Westman (1981) found that many coastal sage scrub species in southern California were affiliated with specific substrates; however, *Artemisia californica*, the dominant species in coastal sage scrub at Gaviota State Park, was not.

Markov models are limited because they make the assumption that transition rates are constant. Our general predictions were based on transition rates that were affected by management practices in the Gaviota State Park region between 1947 and 1989. Livestock grazing ended soon after the establishment of the park in 1967, which was in the middle of our sampling period. Thus the rates we measured would probably be different than those in either heavily grazed or fully protected locations, as a comparison to transition rates outside of the park suggests. Our estimation of the effect of fire on vegetation transition is limited by grouping plots that had burned in 1944, 1956, and 1986, although this was necessary in order to obtain adequate sample sizes on the variable substrates within the park. Plots that burned in 1986 appeared to show exceptionally low grassland to shrubland transition, but otherwise did not produce extreme outliers. Our projected changes in proportions of grassland, shrubland, and *Q. agrifolia* woodlands derived from plots that had burned in different decades were roughly similar to those derived by Scheidlinger and Zedler (1980) in a recently burned area in southern California. Although we found little evidence for other past anthropogenic disturbances in the area now occupied by the park, we cannot exclude them as potential factors that may substantially alter the applicability of our transition rates to either future rates of change or to other geographical locations. Short-term fluctu-

ations in climate (Hansen et al. 1981) could also change transition rates and thus predictions of future community proportions.

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